graphically, measured, and the means and range of variation studied. Statistical tests, such as the *t* and F tests indicate that a normal variation curve would be present if enough specimens were available. From these data it is evident that three factors may be correlated: morphological difference, the season of appearance of the adults, and the rainy season (Turnage and Mallery, 1941) for the area. It is suspected that elevation differences (which also indicate differences in floral ecology) could also be correlated if these data were available with the specimens.

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A REVIEW OF THE TAXONOMY OF THE GENUS EURYDERUS LE CONTE ,1848. WITH NOTES ON THE NORTH AMERICAN DAPTI (OF AUTHORS). (CARABIDAE: HARPALINI)

By George E. Ball [1]

I. Introduction

Among an assortment of carabid beetles from New Mexico which I received for identification some years ago was a specimen of the genus *Euryderus*, which I attempted to determine. I soon found that this was going to be a difficult task, for the specimen did not seem to have the necessary combination of characters to fit any of the couplets in the most recent key available (Casey, 1914: 54–57). The attempt to solve this problem led to the study which is presented in the following pages.

II. Acknowledgements

The following curators made available to me specimens in their care: W. J. Brown, Department of Agriculture, Ottawa (Canadian National Collection); Henry Dietrich,

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Cornell University; and Hugh B. Leech, California Academy of Sciences. E. A. Chapin, formerly of the United States National Museum (presently at the Museum of Comparative Zoology), permitted me to study the Casey types, and P. J. Darlington, Jr., Museum of Comparative Zoology, allowed me to examine the Le Conte type of *Euryderus*. Henry Howden, Department of Agriculture, Ottawa, recently checked some important points for me, and T. J. Spilman, United States Department of Agriculture, provided a microfilm of a reference that could not be obtained at the University of Alberta. M. H. Hatch provided some distributional records, and a copy of the original description of *Amara grossa* Say. The manuscript was critically reviewed by W. G. Evans and Brian Hocking and the final draft was typed by Miss Joan Shore, Department of Entomology, University of Alberta. I am grateful to all of these people for their generous assistance.

III. The Genus *Euryderus*

This genus may be distinguised from the other North American harpalines by the following combination of characters: glossae quadrisetose; paraglossae setose; without specialized vestiture on the ventral surface of the anterior and middle tarsi; anterior tibia flattened and outer apical angle produced into a prominent sharp projection (Fig. 2); lateral margin of pronotum with a row of setae; at least elytral intervals 3, 5 and 7 with a row of large setigerous punctures, the setae long and slender; internal sac of male genitalia with two groups of large spines which are arranged in parallel series, parallel to long axis of median lobe, and a strong "tooth" at right angle to long axis of median lobe (Fig. 1).

Euryderus Le Conte, 1848

1848. *Euryderus* Le Conte, p. 151 [not *Eurydera* Castelnau, 1831]

TYPE SPECIES: *Euryderus zabroides* Le Conte, 1848
[Monobasic]

1848. *Euryderus* Le Conte, p. 371.

1852. *Nothopus* Le Conte, p. 67.

TYPE SPECIES: *Euryderus zabroides* Le Conte, 1848
[Monobasic]

1853. *Nothopus* Le Conte, p. 381.

1854. *Nothopus*, Lacordaire, p. 266, 392.

1868. *Nothopus*, Gemminger and Harold, p. 251.

1881. *Nothopus*, Horn, p. 177.

1883. *Nothopus*, Le Conte and Horn, p. 54.

1900. *Nothopus*, Tschitscherine, p. 342.

1905. *Euryderus*, Cockerell, p. 240.

1910. *Nothopus*, Blatchley, p. 174.

1914. *Nothopus*, Casey, p. 50, 54.

1920. *Nothopus*, Leng, p. 70.

1932. *Euryderus*, Csiki, p. 1081.

1933. *Euryderus*, Leng and Mutchler, p. 80.

1942. *Euryderus*, Van Emden, p. 41 and 73.
1942. *Euryderus*, Jeannel, p. 621.
1945. *Nothopus*, Chu, p. 30.
1951. *Euryderus*, Jaques, p. 50.
1953. *Euryderus*, Hatch, p. 164 and 260.

This synonymy indicates a certain amount of confusion relating to the generic name. Actually, the matter is quite simple, as Cockerell (1906) pointed out. Le Conte (1852: 67) believed that the name *Euryderus* had to be considered as a junior homonym of *Eurydera* Castelnau, and so the new name *Nothopus* was proposed. As a matter of fact, *Euryderus* and *Eurydera* are non-homonymous. *Euryderus* and *Nothopus* are absolute synonyms, and since the former name was published first, it must stand as the correct name for the genus.

IV. The Species

The first species included in *Euryderus* was *zabroides* Le Conte, 1848. In using this name, Le Conte indicated the similarity in form of this species and the members of the Amarini, of which *Zabrus* is a member. In an addendum (1859: 543) to a republication of Say's description of *Amara grossa* (1834: 340) Le Conte suggested that this species may be the same as *zabroides*, but stated that the description of Say was too vague to establish the synonymy with certainty. In 1914, Casey published a major revision of the North American Harpalini, in which he described three new species of *Euryderus*, and a new subspecies of *zabroides* Le Conte. Now, because Casey was able to see four species in a group where previous workers saw only one, and if it is difficult for subsequent workers to recognize these species, then it follows that Casey created the present taxonomic problem. The solution to the problem must then be sought in an analysis of the diagnostic characters used by that author for his new species.

Casey used ten characters in all. Study of the types indicated that four of these characters were unreliable, that is, what Casey stated about the types was not borne out when they were re-examined. These were: the ratio of head width to pronotal length; depth of elytral striae; shape of elytra; and width of the lateral gutters of the pronotum. The six remaining characters were not very impressive, but the variates of each were sufficiently distinct so that they could at least be roughly evaluated. These are listed in Table I.

It seemed that the best way to evaluate the characters was to determine to what extent the variates were correlated. If the combination of variates stated to be typical for each species occurred at a relatively

high frequency, then one could conclude that a number of distinct forms was represented in the genus. This would not prove that each combination was specifically distinct, but would be the first step in such a direction. However, if in additional material these variates were found not to be related as they should be according to the original descriptions, then the basis of recognizing the described entities would be destroyed.

Because four of the six characters to be analyzed could not be assessed numerically, each variate of each character was assigned a letter, depending upon which species it was supposed to characterize. For example, the color "black" was designated by the letter *p*, standing for *privatus* Casey, because this species was the only one of the five named forms diagnosed by Casey as being all black. If a given variate was characteristic of more than one species, for example "punctures of the pronotum numerous and larger anteriorly than posteriorly", then the letter designation depended upon the number of named forms of which the variate was characteristic. The variate cited above was characteristic of *valens*, *zabroides*, *obtusus* and *privatus*. Thus a specimen with this characteristic would be graded v, z, o, p, as shown in Table I. Specimens studied were designated by a letter for each of the variates they possessed and the total number of variates of the six characteristics studied was determined for each specimen (1-v, 1-o, 2-z, 2-a). For purposes of summation, the variates represented by more than a single letter were designated by the letter X (i.e. 1-X). Thus a specimen with "punctures of the pronotum numerous and larger anteriorly than posteriorly" (this variate symbolized by v, z, o, p, as indicated above) received the letter X for this one variate, and the appropriate letter designation for each of the remaining five characters (for example 1-v, 1-o, 2-z, 1-a, 1-X). Intermediate variates were designated by the letter I (i.e. 1-I).

The combinations of variates for specimens which would key to each of the Casey species are presented in Table II. Now, if these species are recognizable, the majority of specimens studied should be found in one of the "typical" groups of combinations. In reality, only four specimens out of 228 were referable to one of the combinations shown in Table II, and these four fitted the *valens* category; the others had such combinations of variates that they could not be referred to any of the named forms. To illustrate this, Table III contains a summary of values assigned to a population sample collected at Medicine Hat, Alberta. Note that not a single specimen can be assigned to any one of the groups indicated in Table II.

These data seem to indicate that the variates are not correlated in the way they should be, if Casey's species have any meaning. Because this

Table I

Symbol Designation of Certain Specific Characters in Euryderus Given by Casey, 1914.

A. COLOR

1. all black ..... p (privatus)
2. black dorsally, labrum black ..... v (valens)
3. rufo-piceous dorsally, labrum black ..... z (zabroides)
4. rufo-piceous dorsally, labrum black medially ..... o (obtusus)
5. rufo-piceous dorsally, labrum all rufous ..... a (arizonicus)

B. FRONTAL IMPRESSIONS OF HEAD

1. elongate, shallow ..... v, z, p
2. broader, shallower ..... o
3. punctiform ..... a

C. PRONOTAL FOVEAE

1. distinct from marginal grooves, deeper ..... a
2. continuous with marginal grooves, shallower ..... v, z, o, p

D. PRONOTAL PUNCTURES

1. few posteriorly, very few to absent anteriorly ..... a
2. numerous and larger anteriorly and posteriorly ..... v, z, o, p

E. ELYTRA: L/W

1. 1.18–1.26 ..... o
2. 1.27–1.36 ..... v, z, p
3. 1.37–1.40 ..... a

F. SETAE OF THE ELYTRA

1. 72–90 in odd intervals, evens with a few apically ..... a
2. 18–28 in odds, none in evens ..... p
3. less than 72 in odds, none in evens ..... z
4. less than 72 in odds, a few in evens v

is so, I conclude that Casey's arrangement is incorrect, and that all of the names proposed by him apply to individuals of the same species. The oldest trivial name available is *grossa* Say 1834 (Amara), and it is sufficiently clear from the original description that this name indeed

TABLE II

Combinations of Variate Symbols of Specimens of Euryderus Which Would Key to The Casey Species.

1. 2-v, 4-X; or 1-v, 1-I, 4-X	*valens*
2. 2-o, 3-X; (only 5 variates given in key)	*obtusus*
3. 2-z, 4-X; or 1-z, 1-I, 4-X	*zabroides*
4. 2-p, 4-X	*privatus*
5. 6-a	*arizonicus*

applies to the single species of *Euryderus*, the opinions of Le Conte and Casey notwithstanding. Therefore, the synonymy of this species is as follows:

EURYDERUS GROSSUS (SAY, 1834)

Amara grossa Say, 1834: 430 ("inhabits N.W. Terr.")—Say, 1859: 543.—Le Conte, 1859: 543.—Casey, 1914: 57.

Nothopus grossus, Gemminger & Harold, 1868: 251.—Blatchley, 1910: 174.

Euryderus grossus, Csiki, 1932: 1081.—Hatch, 1953: 164, 260 (fig. adult).

Euryderus zabroides Le Conte, 1848: 151; type, MCZ No. 5871, locality label a green disc ("Neb etc"), Le Conte Coll. Museum of Comparative Zoology, Harvard University.—_____, 1848: 371.—Csiki, 1932: 1081.—Van Emden, 1942: 41 & 73 (larva).—Hatch, 1953: 164.

Nothopus zabroides Le Conte, 1852: 67._____, 1853: 381. Gemminger & Harold, 1868: 251.—Le Conte & Horn, 1883: 54.—Blatchley, 1910: 174. Casey, 1914: 57; Leng, 1920: 70.—Csiki, 1932: 1081.—Chu, 1945: 30 (fig of larva).

Nothopus valens, Casey, 1914: 55, Type specimen, USNM No. 47727, labelled "Ia.", Casey Coll., United States. National Museum. NEW SYNONYMY.—Leng, 1920: 70.—Csiki, 1932: 1081.

Euryderus valens, Csiki, 1932: 1081.—Jaques, 1951: 50.

Nothopus obtusus Casey, 1914: 56, Type specimen, USNM No. 47729, labelled "Col.", Casey Coll., United States National Nuseum. NEW SYNONYMY.—Leng, 1920: 70.

Euryderus obtusus Csiki, 1932: 1081.

Nothopus zabroides privatus Casey, 1914: 56; Type specimen USNM No. 47726, labelled "Tex.", Casey Coll., United States National Museum. NEW SYNONYMY.—Leng, 1920: 70.

Euryderus privatus, Csiki, 1932: 1081.

Nothopus arizonicus Casey, 1914: 56; Type specimen, USNM No. 47728, labelled "Ariz.", Casey Coll., United States National Museum.—Leng, 1920: 70.

Euryderus arizonicus, Csiki, 1932: 1081.—Van Emden, 1942: 73 (as a synonym of *zabroides* Le Conte).

TABLE III

Combinations of Variate Symbols of Euryderus Specimens From Medicine Hat, Alberta

2-v, 1-o, 3-a	1-v, 1-o, 2-a, 1-I, 1-X	2-o, 1-z, 2-a, 1-I
2-v, 1-o, 2-a, 1-X	1-v, 2-a, 3-X	2-o, 1-a, 2-I, 1-X
2-v, 1-o, 2-a, 1-I	1-v, 1-o, 1-a, 1-I, 2-X	2-o, 1-a, 3-X
1-v, 2-o, 2-a, 1-I	1-v, 1-o, 3-a, 2-X	1-o, 1-a, 1-I, 2-X
1-v, 1-o, 1-z, 2-a, 1-I	1-v, 2-a, 1-I, 2-X	1-o, 1-z, 1-a, 1-I, 2-X
1-v, 2-a, 2-I, 1-X	1-v, 1-z, 2-a, 2-X	1-o, 1-p, 1-a, 3-X
1-v, 3-a, 1-I, 1-X	1-v, 1-a, 1-I, 3-X	1-o, 1-a, 1-I, 3-X
1-v, 1-o, 1-z, 2-a, 1-X	1-v, 1-a, 1-I, 1-X	1-z, 1-p, 2-a, 2-X
1-v, 1-o, 2-a, 1-I, 1-X	1-v, 1-o, 4-X	1-p, 1-a, 4-X

V. GEOGRAPHICAL VARIATION

The following observations do not constitute an exhaustive review because they are based on the few specimens that were readily available to me, and because I have considered only those characters which have been used as a basis for diagnosis of taxonomic units within this genus. The analysis shows the geographical pattern for each character. Variation in the majority of these characters is difficult to describe accurately because the variates tend to grade into one another. This does not apply

to variation in the number of setigerous punctures on the elytra, and so this aspect is dealt with in more detail.

The total number of elytral punctures on a single specimen varies from 30 (Dallas, Texas) to 107 (Medicine Hat, Alberta). Sample means range from 40 (Dallas, Texas, N = 18) to 92 (Clear Creek, Colo., N = 3). When the samples are compared, a continuum of variation is seen, but one which does not appear to comprise a simple cline. The lowest average values occur in the British Columbia, Kansas and Arkansas samples; the highest values are represented by the Colorado and Arizona samples. The variation pattern is analyzed in detail, using the number of punctures in the even-numbered intervals only. This variate was chosen rather than the total number of punctures for two reasons. First, the observed pattern is principally the result of variation which occurs in the number of punctures in the even intervals, and so emerges more clearly, if the even intervals are considered independently. Second, there is a general correlation between the total number of elytral punctures and the number of punctures in the even intervals alone. Thus the sum of the punctures in the even intervals is a useful index of the total number of punctures. Therefore, it is unnecessary to present details for variation in the latter character.

Data on variation in the number of punctures in the even intervals are presented in Table IV. These values represent the number of punctures in the even intervals of both elytra. The sexes were pooled for purposes of this analysis because variation in this character appears to be independent of sex. Statistical parameters are presented for samples of 10 or more. The mean values are very low for samples from Kansas (excluding *Medora*), eastern Texas, and Arkansas; they are slightly higher for the Osoyoos, British Columbia sample and higher still for El Paso, Texas, and Medora, Kansas. The mean values are appreciably higher again for the remainder of the samples. Another fact to be derived from Table IV is that the samples having the lowest means also exhibit relatively slight variation. Coefficients of difference were calculated for the larger samples to assess the taxonomic significance of the observed differences. Values are presented in Table V. Those over 1.28 signify that more than 90 per cent of the curves of variation do not overlap for the two populations for which the values were calculated. Such pairs of samples are "taxonomically different" at the subspecies level (Mayr, Linsley & Usinger, 1953: 146). Values around 1.23 indicate that about 88 per cent of the compared samples do not overlap; for values around 1.04 there is joint non-overlap of 85 per cent; the very low figures indicate a wide overlap of the sample curves.

These data seem to indicate that the Medicine Hat, Aweme, Denver, and Colorado Springs population samples form a group distinct from the

Table IV

Data on Geographical Variation in Total Number of Setiferous Punctures in Even-Numbered Elytral Intervals in Euryderus Grossus Say.

LOCALITY	N	RANGE	MEAN	S.D.
Osoyoos, B. C.	3	0–2	0.67	
Empress, Alta.	2	7–10		
Medicine Hat, Alta.	27	0–28	9.15±1.38	7.18
Lost River, Alta.	4	5–41	21.20	
Rutland, Sask.	2	5–19		
Pine Lake, Sask.	3	1–14	7.67	
Canora, Sask.	8	2–17	6.12	
Great Sand Hills, Sask.	4	11–15	14.80	
Aweme, Man.	11	1–23	10.73±3.23	7.44
Hill City, S. D.	3	8–12	9.33	
Valentine. Neb.	5	3–12	8.20	
Chesterton, Ind.	5	2–16	8.40	
Denver, Colo.	16	0–24	9.94±1.52	6.08
Colorado Springs, Colo.	10	0–26	10.00±2.89	9.14
Clear Creek, Colo.	3	4–13	9.33	
Pueblo, Colo.	9	4–26	12.56	
Rocky Ford, Colo.	4	1–14	8.75	
Las Vegas, N. M.	6	6–16	11.83	
Kavenata, Ariz.	3	7–25	14.33	
Chiricahua Mts., Ariz.	6	4–19	10.17	
El Paso, Tex.	7	0–4	1.20	
Medora, Ks.	3	0–7	2.67	
Sedgwick Co., Ks.	8	0–1	0.12	
Pottawattomie Co., Ks.	18	0–1	0.11±0.07	0.31
Dallas, Tex.	12	0–1	0.08±0.01	0.21
Hope Co., Ark.	5	0	0.00	

TABLE V

Coefficients of Difference Between Some Population Samples of Euryderus Grossus.

	Aweme	Denver	Colorado Springs	Pottawattomie Co., Ks.	Dallas, Tex.
Medicine Hat	0.11	0.005	0.005	1.21	1.23
Aweme		0.005	0.004	1.40	1.39
Denver			0.006	1.54	1.57
Colorado Springs				1.05	1.06
Pottawattomie Co., Ks.					0.06

Pottawattomie County and Dallas, Texas samples which form a second group. This latter group is very different from the Aweme and Denver samples; less different from the Medicine Hat sample, and still less different from the Colorado Springs sample. The observed differences are not exactly correlated with geographical distance between samples. For example, Denver is about half way between Medicine Hat and Dallas. If the pattern of variation were a gentle cline, then the mean of the Denver sample would be about mid-way between the means of the other samples in question. The fact is that the Denver and Medicine Hat samples are hardly different, while both are markedly different from the Dallas sample.

Another factor to consider besides total number of punctures in the even elytral intervals is the relative frequency of punctate and impunctate individuals throughout the range of the species. (The terms "punctate" and "impunctate" are used here only with reference to the even-numbered

intervals.) Thus the number of variates is reduced to two, and this has the effect of increasing the statistical importance of individual specimens. Data are presented in Figure 3. The numerators of the fractions on this map represent the number of specimens from one locality which lack punctures in the even intervals. The denominator represents the total number of individuals comprising the sample. The triangles stand for localities which are represented by single specimens: white for impunctate; black for punctate specimens. The triangle in Colorado, one-half of which is black, represents two specimens each from a different but adjacent locality. Figure 3 shows that a substantial percentage of Kansas-eastern Texas specimens are impunctate. This applies generally also to individual specimens from the adjacent areas. Two of three individuals collected at Osoyoos, B. C. lack punctures. The remaining British Columbia specimens are punctate (a total of five in one individual, fewer than that in the remaining). Throughout the rest of the area, the punctate condition predominates. The El Paso (type locality of *E. privatus* Casey) sample occupies an intermediate position both geographically and with respect to this character distribution. This locality may be marginal for the complete expression of the "punctate" variate. This same statement applies to specimens from western Oklahoma and western Kansas, and probably also to the specimens from south-central British Columbia.

Thus the samples of *Euryderus grossus* may be placed in one of two categories, depending upon whether or not the even elytral intervals are punctate. The impunctate samples occupy the southeastern periphery of the total range of *grossus*, and the very limited material from British Columbia suggests that the northwestern periphery also has a considerable proportion of this phenotype. This statement requires further comment. Although only two out of six B. C. specimens are impunctate, the others have very few punctures in the even intervals. This condition is common in those population samples where the majority of specimens are impunctate. This is why I consider it likely that populations which occupy southern British Columbia are phenotypically similar to those which occupy the Kansas-Texas area. Elsewhere, the punctate phenotype predominates. Probably relatively steep clines formed by geographically intermediate populations bridge the gaps in means which are shown in the data.

This distribution of characters can be interpreted as a central-peripheral one (Brown, 1958). In terms of this hypothesis, I suggest that the impunctate phenotype is the older, and that it has been replaced in the center of the range by the more recently evolved "punctate" type. Presumably the replacement process has gone farther in the northwest than

it has in the southeast. The assumption that the impunctate phenotype is more primitive is based on the fact that the majority of harpalines are impunctate, and so specialization would be a departure from this norm. The greater the number of punctures, the greater the specialization, and thus the farther is the departure from the ancestral condition. Conversely the less specialized type would be characterized by fewer punctures. Implicit in this hypothesis is the assumption that the punctate variate is adaptively superior to the impunctate one, or at least that it is an external manifestation of a more favorable genetic combination. I have no information which bears on this vital point.

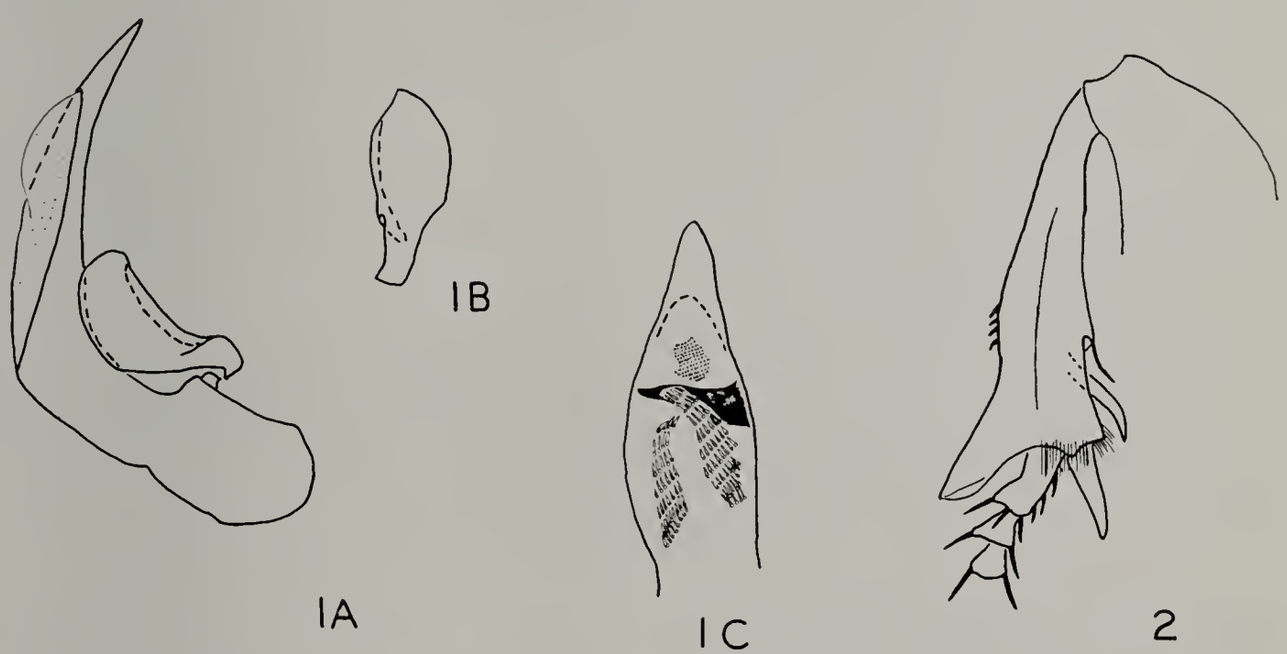

FIG. 1 Male genitalia of *Euryderus grossus* (Say), El Paso, Texas, July 27, 1919, J. C. Bradley (CU). A. Median lobe, left lateral aspect, actual length, base to apex, 3.2 mm.; and left lateral lobe *in situ*. B. Right lateral lobe, ventral aspect. C. Apical portion of median lobe, ventral aspect, showing spine series and tooth of internal sac *in situ*. FIG. 2 Right front tibia of *Euryderus grossus* (Say), Hope, Arkansas (CU).

An alternative hypothesis to the one presented above is that the punctate variate is the more primitive one, at least in *Euryderus*, and that more recently, parallel mutations have occurred and have been selected for independently toward the southeastern and northwestern periphery of the range of the species. Such mutations led to the reduction in the total number of punctures, especially in the even intervals. These alternatives can be tested, but only indirectly, in terms of population genetics and experimental ecology.

Color of the integument varies from wholly black to completely rufopiceous. Many specimens are intermediate between these extremes, with some parts of the body darker than others. Both extremes occur throughout the range of the species. In the samples from British Columbia, Alberta,

Saskatchewan, Manitoba, western Texas, and Arizona, intermediate specimens predominate. In Kansas and eastern Texas, black specimens are more numerous, but in Arkansas, which is still farther east, the specimens are all relatively pale. The importance of this variation is difficult to assess because black grades into rufo-piceous, and it is often difficult to decide how to classify a given specimen. Also, color is known to change ontogenetically, so a pale specimen may be such only because it was killed before the cuticle had sufficient time to darken. Therefore, one must wonder how accurately the observed differences reflect real differences among the gene pools of the various populations.

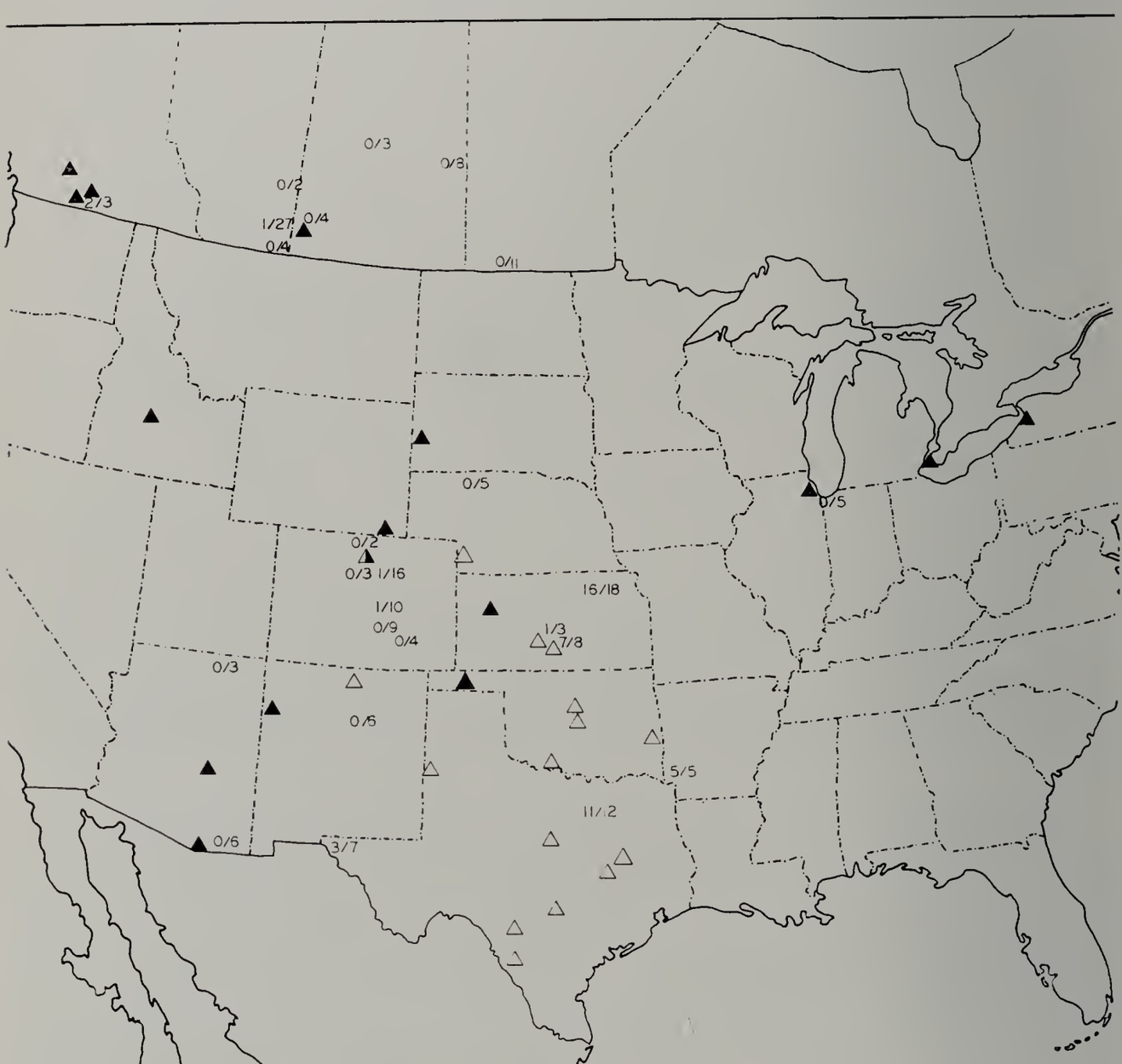

Fig. 3 Map showing distribution of *Euryderus grossus* (Say). Empty Triangles represent single specimens which lack setigous punctures in the even-numbered elytral intervals. Filled Triangles represent single specimens which have setigerous punctures in the even-numbered elytral intervals. Fractions stand for localities represented by more than one specimen: denominators are the total number of specimens, numerators are the number of specimens which lack punctures in the even numbered elytral intervals.

Three variates in the relative development of the frontal impressions are recognized. (See Table I.) All three variates occur in the Medicine Hat and Pottawattomie County samples. The punctiform variate is the most frequent in the Arkansas and Pottawattomie County samples (over 50 percent in both). In the rest of the samples, including the one from Dallas, Texas, over one-half of the specimens have either elongate-shallow or broader-shallower impressions, with the latter variate predominating slightly.

Variation in the postero-lateral impressions of the pronotum is divided into two classes: shallow and continuous with the lateral margins; or deeper and isolated from the lateral grooves. Both variates occur throughout the range of the species. In the Pottawattomie County sample, the "isolated" condition occurs in 18 of 19 specimens; in the Dallas and Medicine Hat samples, the two variates occur in about equal frequency; in the remaining samples, the "continuous" variate is more frequent, and in several of these samples, the "isolated" variate is not represented.

Punctation of the dorsal surface of the pronotum is divided into two classes "punctures finer and fewer", or "coarser and more numerous". Both are found throughout the range of the species, but at Medicine Hat and localities in the Mississippi Basin, the punctures of most specimens are in the "finer and fewer" class, while throughout the rest of the range, the "coarser, more numerous" class predominates.

I have two observations to make concerning the characters other than those of elytral punctation. The first is that their patterns of variation are discordant with respect to each other. That is, populations which are similar with respect to one of these characters are different with respect to another character. This fact lends support to the statements of Wilson and Brown (1953) regarding the nature of geographical variation, and indicates that subspecies need not be recognized in this species. The second observation is that these variates are defined subjectively, and it would be difficult to define them objectively. Therefore, it is likely that another worker might classify some specimens differently than I have, and so a pattern of variation different from the one I have indicated could be shown. Since this is so, it would seem that a more detailed analysis is unwarranted.

This study of geographical variation was based on a total of 228 specimens, collected in the localities listed below. These are in alphabetical order by state and province, and by county within each state. The letters in parentheses following each citation represent an abbreviation for the institution from which the specimen was borrowed. They are as follows:

CAS - California Academy of Sciences, San Francisco.

CNC - Canadian National Collection, Department of Agriculture, Ottawa.

CU - Cornell University, Ithaca, New York.

GEB - collection of the author.

UA - University of Alberta, Edmonton, Canada.

The greater part of this material was collected during June, July and August. Extreme dates are: April 1 (Sedgwick, Ks.) and December 22 (Oklahoma City, Okla.).

CANADA

ALBERTA. 2.6 mi. w. Empress (GEB); Medicine Hat (UA), (CNC), Lost River, D.R.E. Stn. (CNC); Seven Persons (CNC).

BRITISH COLUMBIA. Kamloops (CNC); Keremeos (CNC); Oliver (CNC); Osoyoos (CNC); Osoyoos Lake, (CNC).

MANITOBA. Aweme (CNC).

ONTARIO. Point Pelee (UA).

SASKATCHEWAN. Canora (CNC); Crane Lake (CNC); Great Sand Hills, 50° 8′, 109° 16′ (CNC), Pike Lake (CNC); Rutland (CNC).

UNITED STATES

ARIZONA. COCHISE CO: Chiricahua Mts. (CAS). GILA CO: Miami (CAS). NAVAJO CO: 19 mi. s.w. Keyanata, 6500′ (CAS). PIMA CO: Nogales (CAS). County not determined: Webb (CAS).

ARKANSAS. HEMPSTEAD CO: Hope (CU).

COLORADO. CLEAR CREEK CO: Clear Creek (CAS). DENVER CO: Denver (CAS). EL PASO CO: Colorado Springs (CU & CAS). LARIMER CO: Fort Collins (CAS); Loveland (CAS); Poudre CANYON, 5200′ (GEB). OTERO CO: Rocky Ford (CU). PUEBLO CO: Pueblo (CU). County not determined: Rock Creek.

IDAHO. "Idaho" (CAS).

ILLINOIS. COOK CO: Chicago (UA).

INDIANA. PORTER CO: Chesterton (CAS).

KANSAS. "GOVE CO., 2500′"(CU). HARVEY CO: Sedgwick (CAS). POTTAWATTOMIE CO: Blackjack Creek, (GEB); Little Gobi Desert (GEB). RENO CO: Hutchinson, (CAS); Medora (CU & CAS). STAFFORD CO: salt flats area (GEB).

NEBRASKA. CHASE CO: Imperial (CAS). CHERRY CO: Valentine (CAS).

NEW MEXICO. BERNALLILO CO: Albuquerque (CNC). MCKINLEY CO: Pinedale (GEB). SAN MIGUEL CO: Las Vegas (CAS). TAOS CO: Aztec, Animas Valley (CAS).

NEW YORK. ERIE CO: Buffalo (CU).

OKLAHOMA. "COTTON CO.", (CAS). LE FLORE CO: Wichita Natl. Forest, (CAS). LOGAN CO: Guthrie (CU). OKLAHOMA CO: Oklahoma City (CAS). "TEXAS CO." (CAS).

OREGON. "N.E. Oregon"—(Hatch, 1953: 165).

SOUTH DAKOTA. PENNINGTON CO: Hill City (CAS).

TEXAS. BAILEY CO: Muleshoe (CAS). COMAL CO: New Braunfels (CU). COMANCHE CO: Comanche (GEB). DALLAS CO: Dallas (GEB, CAS). DIMMIT CO: Carrizo Springs (CAS). EL PASO CO: El Paso (CU). "LEON CO." (CAS). ROBERTSON CO: Hearne (CAS). UVALDE CO: Uvalde (CAS).

WYOMING. LARAMIE CO: Cheyenne (CU).

WASHINGTON. M. H. Hatch (*in litt.*) gives the following records: Old Fort Okanagan, Vashon Island, and Walla Walla.

VI. Classification of the Genus *Euryderus*.

The position of *Euryderus* in the harpaline system has been unstable. This is a reflection of the general instability of the arrangement of the genera of this large tribe, the members of which are sufficiently varied to suggest that they represent a number of distinct lines of evolution, but which are sufficiently uniform so that it is very difficult to decide what the lines are, and thus to classify the group. In certain sections of the Harpalini it is difficult even to draw generic limits. This is particularly true of some groups which are close to *Harpalus*, such as *Megapangus*, *Ophonus*, *Opadius* and *Glanodes*. Within the last 78 years, seven classifications of the Harpalini have been represented. Six of them are reviewed briefly here, especially with reference to *Euryderus*.

The principal feature used to classify the harpaline genera is the degree of development of the front and middle tarsi of the males, and the nature of the vestiture of the ventral surface of these articles. Jeannel (1941: 45-47) recognizes two types of vestiture: spongy and serial. Both types are found in the Harpalini, and further, some forms lack any specialized vestiture. The anterior tarsi are usually broadened considerably in forms which have well developed vestiture. If the vestiture is lacking, usually the tarsal articles are not expanded. (It would be interesting to know something about the genetic changes which led to suppression of the secondary sexual

characters in this group.) If a classification of the Harpalini is based on the nature of the front tarsi of the males, then three groups of genera may be made: those with widened tarsal articles, and having spongy vestiture below; those with widened articles, and serial vestiture; and those with the articles narrow, and with or without vestiture. The earliest useful classification (Le Conte, 1853: 381) which was amplified by Horn (1881: 174-185) grouped the genera in just this fashion. The group with reduced vestiture or none at all was called the Dapti. Tschitscherine (1900) reviewed Horn's work, and presented a revised classification. Tschitscherine pointed out that the absence of vestiture from the anterior tarsi of males was not a a reliable criterion of relationship, because this character varied within a single genus (*Acinopus*—subgenus *Acmastes* without tarsal vestiture, typical subgenus with this vestiture), and also that otherwise very similar genera could be distinguished by the presence or absence of vestiture (*Harpalus*—with vestiture, *Harpalobrachys*—vestiture lacking). The Daptini was restricted to include those genera having unspecialized maxillae, bisetose glossae, and glabrous paraglossae. Thus, *Piosoma* and *Euryderus* (*Nothopus*, Tschitscherine) were removed from the Daptini and were placed near *Harpalus* in the Harpalini (*s. str.*)[1]

Casey (1914:49), who apparently overlooked or ignored Tschitscherine's important study, included *Euryderus* and *Piosoma* in the Daptini, on the basis of the structure of tarsus in the males.

Csiki (1932) distributed the Dapti of Horn among seven of his 21 subtribes, and *Euryderus* was placed in a subtribe of its own, the Euryderi. According to Van Emden (*in litt.*, 1956), the groups used by Csiki were suggested to him by Schauberger; unfortunately they were never defined.

Jeannel (1942: 584 *et seq.*) presented a classification of the Harpalini (accorded family rank by him), based on a variety of characters, including the form of the male genitalia and the number of setae on the penultimate article of the labial palpus. This author divided the Harpalidae into six subfamilies, one of which, the Harpalitae, contained the Harpali and Dapti of Horn, minus the genera in which the penultimate article of the labial palpus was bisetose. The palaearctic Harpalitae were arrayed in five tribes, and Jeannel stated specifically that *Euryderus* belonged to the Tribe Selenophorini. This group included those Harpalitae with narrow glossae, frons without a pair of longitudinal grooves, and median lobe symmetrical, the membranous dorsal area not restricted to the left side (1942: 621). In the key (1942: 615) Jeannel used also the presence of pubescence to

[1] Although the group-names as used by Tschitscherine end in -ini, he refers to them as subtribes of the Tribe Harpalini.

distinguish French selenophorines from harpalines. When he placed this genus in the Selenophorini, Jeannel may have considered the elytral hairs of *Euryderus* to represent pubescence. However, the form of the male genitalia indicate that this genus should have been placed among the Harpalini (*sensu* Jeannel).

Basilewsky (1946) presented a classification of the African Harpalinae (equivalent to the Harpalini of Horn, Tschitscherine, Leng, Csiki, and to the family Harpalidae of Jeannel) which was similar to Jeannel's. The constitution of the typical group was the same (i.e. Harpalitae of Jeannel and the equivalent Harpalini of Basilewsky). However, Basilewsky defined differently the selenophorine group, a result of which was that some genera listed by Jeannel as selenophorines were shifted to the harpaline group, and *vice versa*. The principal character used by Basilewsky to distinguish between the two groups was the length of the metatarsus of the hind leg; as long or longer than articles two plus three in selenophorines; shorter than articles two plus three in the harpalines. Basilewsky also mentioned that in most of the genera of the Harpalina the median lobe was inclined to the left; rarely was this condition found in the Selenophorina. In *Euryderus*, the hind metatarsus is shorter than the combined lengths of the next two articles, and, on the basis of this character, this genus must be considered to be a harpaline rather than a selenophorine.

Van Emden (1953: 513–519) discussed the classification of the Neotropical Harpalini (*sensu* Horn). He recognized a total of five subtribes, and within the Harpalina, he recognized at least two supergenera: Harpali and Selenophori, the equivalents of the Harpalina and Selenophorina of Basilewsky. His definition of the Selenophori excluded *Euryderus* from this group. In a letter to me dated November 5, 1956, van Emden stated that excluding the tarsal vestiture, "*Euryderus* seems to me to be quite a typical member of the Harpali, with its short hind tarsi, short first segment of these, absence of seriate punctures from the striae, and strongly setulose paraglossae." I agree with this conclusion. While none of these characters is conclusive proof in itself that *Euryderus* is a harpaline (in the strictest sense), the combination of them plus the form of the male genitalia makes it seem virtually certain that *Euryderus* must go in the same group as *Harpalus*.

Three other "daptine" genera appear not to be properly classified at present. These are *Piosoma* Le Conte, 1848; *Carthacanthus* Dejean, 1829; and *Geopinus* Le Conte, 1848. *Piosoma* resembles *Euryderus* in having long setae on the elytra which arise from large punctures in the elytral intervals; the paraglossae are fringed with setae; the hind metatarsus is short and the internal sac of the male genitalia bears two large spines;

and the membranous dorsal portion of the median lobe is restricted to the left side. The fourth article of the front tarsus of the male bears two rows of serially arranged specialized vestiture. This genus without doubt is also a harpaline in the strictest sense (as Tschitscherine stated) and is not a member of the Daptini (Casey, 1914:50) or of the Diorychi (=Selenophori) as Csiki (1932: 1194) suggested.

A second genus, *Cratacanthus*, was placed in the Harpalina (Tschitscherine, 1900: 340), in the Acinopi (Csiki, 1932: 1091), and also in this group by Jeannel (1942: 618). The Acinopi are harpalines with large heads, short hind metatarsi, and symmetrical male genitalia. *Cratacanthus* has these characters. However, in this genus, the apical opening in the median lobe is to the left, as in the Harpalina. Another interesting point is that the larva of this genus and of *Euryderus* are more similar to one another than either is to any other harpaline (van Emden, 1942: 41). Thus I suggest that *Cratacanthus* should also be included in the Harpali. The males of a third genus, *Geopinus*, have spongy pubescence on the underside of the front tarsi; the male genitalia are not inclined to the left, and the hind metatarsus is short. I suggest that *Geopinus* is, in fact, an anisodactyline, perhaps an aberrant one. None of its other structural characters precludes such an association. Like *Euryderus*, this genus was placed in a group of its own by Csiki (1932: 1026). Tschitscherine (1900: 340) associated *Geopinus* with *Daptus* in his Daptini.

Another "daptine" genus requiring brief mention is *Glanodes* Casey, 1914. Csiki (1932: 1185) listed this taxon as a subgenus of *Harpalus*. I have studied specimens representing *Glanodes*, and concur with this allocation.

The form of the legs and tibial spurs of the genera discussed above suggests that these appendages are adapted for digging. This statement also applies to the other "original" daptines. Perhaps the reduction of the fore and middle tarsi in the males and the loss or reduction of vestiture is correlated with a fossorial mode of life.

It is my opinion that the classification and the rank of taxonomic categories of the Harpalini presented by van Emden (1953) for the South American Harpalini are sound, and that they can be applied with little modification to the North American fauna. Of course, there are no "typical" Harpali in South America, whereas members of this group abound in North America.

VII. Summary

1. The correct name for this genus is *Euryderus* Le Conte, 1848, not *Nothopus* Le Conte, 1852.

2. An analysis of variation of characters claimed to be diagnostic of species indicates that *Euryderus* is represented in North America by a single species: *grossus* Say, 1834.

3. Synonyms of this species are: *zabroides* Le Conte, 1848; *valens* Casey, 1914; *privatus* Casey, 1914; *obtusus* Casey, 1914; *arizonicus* Casey, 1914.

4. Geographical variation of number of punctures in the even elytral intervals seems to form a central-peripheral pattern.

5. *Euryderus* is a member of the supergenus Harpali, subtribe Harpalina.

6. *Piosoma* Le Conte, 1848 and *Cratacanthus* Dejean, 1829 also belong in the Harpali.

7. *Geopinus* Le Conte, 1848 belongs in the subtribe Anisodactylina.

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